A Review of the Pleistocene History of the Orang-Utan (*Pongo* Lacépède 1799)

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H. D. KAHLKE

Fossil remains of the great Pongidae are very rare in Africa as well as in southern Asia and, therefore, it is not yet possible today to draw the outlines of a pleistocene history of *Pan* (Oken 1816) or *Gorilla* (Geoffroy 1852) on account of the lack of fossil documentation. In the case of *Pongo* (Lacépède 1799), however, quite a number of pleistocene localities with fossil remains of the genus are on record—even of different geological horizons. These data enable us to attempt a review of the pleistocene distribution, phylogeny, and taxonomy of this genus.

The presence of *Pongo pygmaeus pygmaeus* (Hoppius)—a large orang indistinguishable from the pleistocene form *Pongo pygmaeus "weidenreichi"* (Hooijer), either by size or by dental morphology—in the younger unconsolidated cave-filling of Hang-Hum, Luc-Yen, DR Viet Nam, proves the animal still to have been living on the continent of southeast Asia in post-pleistocene times.

Fossil Record of Pleistocene and Early Post-Pleistocene *Pongo*

Altogether we know today 18 pleistocene fossil localities with *Pongo* in southern and southeastern Asia, namely from South China (7); DR Viet Nam (4); Laos (3); Sarawak (1); and Java (3). Post-pleistocene localities with "prehistoric" *Pongo* remains have been published from Sumatra (3) and Kalimantan (1), and in Viet Nam one locality (Hang-Hum, post-pleistocene layer) was discovered in 1964. Sources for details on these sites are as follows:

China

Lengchaishan Cave (Plate I) (Young and Chow 1956:608–609; Pei 1957:65; 1962:211; Pei and Woo 1956:477–490; Kahlke 1961*a*:86; 1961*b*:53; 1962:97; Woo 1962:65.

H. D. Kahlke is affiliated with the Institute of Quaternary Palaeontology, Weimar, GDR.

Hoshantung Cave (Young 1932:385; Weidenreich 1937:30–31; Bien and Chia 1938:325; Pei 1939:126; Hooijer 1948:177; Kahlke 1961*a*:84; 1961*b*:51.

Newshuishan Cave (Young and Chow 1956:608–609; Pei and Woo 1956:489; Pei 1957*a*: chart IV; 1957*b*:65; 1960:10; Kahlke 1961*a*:87; 1961*b*:54; 1962:102; Woo 1962:65.

Shaoshin Cave (Chang 1959:141–143; Kahlke 1961*a*:92; 1961*b*:62.

Zhaicun Cave (Wu, Chao, Yuan and Shen 1962:412).

Shuang Cave (Liu 1962:202).

Feishu Cave (not published. There are a few more recently discovered fossil localities with *Pongo* in southern China [information by Prof. Dr. Woo Ju-Kang in Peking, December 1964] indicating that the border of northernmost distribution of pleistocene *Pongo* is somewhat more to the north. The data from these localities have not as yet been published).

DR Viet Nam

Hang-Hum Cave (Plate II) (Kahlke and Nguyên van Nghiâ 1965:15).

Tan-Van Cave (Plate III) (discovered in 1964; data not published).

Thung-Lang Cave (Fromaget 1941:63; Saurin 1950:259; 1951:534).

Hang-Quit Cave (discovered in 1964; data not published).

Laos

Tam-Hang Cave (Fromaget 1936*a*:740; 1936*b*:785; 1940*a*:52; 1940*b*:60; 1941:63; Fromaget and Saurin 1936:10; Arambourg and Fromaget 1938:793–795; Saurin 1951:534).

Tam-P'a-Loi Cave (Fromaget and Saurin 1936:12; Saurin 1951:534).

Houei-Hoc Cave (Saurin 1942:153; 1950:259).

Kalimantan

Niah Cave (Harrisson 1957:161; 1958:549; 1959:2; 1960:448; Koenigswald 1958:620; Medway 1959*a*:627; 1959*b*:151; Solheim 1960:84; Hooijer 1960*a*:408; 1962*b*:485; Hemmer and Koenigswald 1964:10).

Sumatra

Sibrambang Cave, Lida Ajer Cave, Djamboe Cave (Dubois 1891:93; Hooijer 1946:17; 1947:254; 1948:177; 1960*b*:39; 1962*b*:25; Hemmer and Koenigswald 1964:10).

Java

Sangiran (Koenigswald 1939:35; 1940:63; Hooijer 1948:272; 1952:440; 1956:7; 1957:6; Kahlke 1962:99).

Trinil (Dubois 1891:94; 1895:739; 1896*a*:23; 1896*b*:16; 1896*c*:2; 1896*d*:268; Turner 1895:424; Topinard 1895:605; Gregory 1916:320; Gregory and Hellman 1923:526; Miller 1923:527; Koenigswald 1936:729; 1939:38; 1940:41; Weidenreich 1937:145; Hooijer 1948:272; 1952:440; 1956:7; Kahlke 1962:103).

Punung fissures (Koenigswald 1939:37; Badoux 1959:150).

FOSSIL HISTORY OF THE GENUS *Pongo*

A survey of the fossil history of the genus *Pongo* leads back from the sub-recent populations of Sibrambang, Lida Ajer, and Djamboe caves (Sumatra), Niah Cave (Horizon II, Kalimantan), and Hang-Hum Cave (Horizon II, Viet Nam), to the late pleistocene populations of the Punung fissures (Java), Tam-Hang, Tam-P'a-Loi, and Houei-Hoc caves (Laos), Hang-Quit, Hang-Hum (Horizon I), and Thung-Lang caves (Viet Nam), Hoshantung, Newshuishan, Shaoshin, Zhaicun, Shuang, and Feishu caves (southern China), to the middle pleistocene populations of Trinil (Java) and Tan-Van (Viet Nam), and lastly to the early middle pleistocene populations of Djetis (Java) and Lengchaishan Cave (southern China).

However, there is no earlier unambiguous fossil record of the genus *Pongo* or the line leading to it. It is, nevertheless, evident that earlier and more primitive forms of the *Pongo* line must have existed. There are, finally, various speculations on the earlier history of *Pongo* due to some fragmentary Siwalik primate fossils, of which often—to quote the late E. Dubois (1897:83)—it does not even seem possible to determine the genus with certainty. In deciding the position which these Siwalik fossils have to occupy in the genealogical scheme of the Pongidae, we are met with numerous opinions and difficulties, arising from the scanty nature of the fossil material itself. The fossils under consideration are:

Upper caninus from the upper Siwaliks (original lost)

Pithecus cf. *satyrus* Linnaeus (Falconer 1868, I:304)
Pithecus satyrus Linnaeus (Falconer 1868, II: 578)
Primates gen. et sp. indet. (Dubois 1897:83)
Primates gen. et sp. indet. (Branco 1898:6)
Simia cf. *satyrus* Linnaeus (Pilgrim 1910:198; 1913:325; 1915:2; 1927:21)
Simia satyrus Linnaeus (Matthew 1929:443)
Simia cf. *satyrus* Linnaeus (Colbert 1935:59)
Simia cf. *satyrus* Linnaeus (Terra 1943:459)
Primates gen. et sp. indet. (Hooijer 1948:290)
Primates gen. et sp. indet. (Colbert and Hooijer 1953:18)
Primates gen. et sp. indet. (Badoux 1959:118)

As has been suggested by Dubois (1897) and Branco (1898) and accepted by the more recent authors, this lost specimen should be classified as "Primates gen. et sp. indet."

M_3 dex., Indian Museum, Calcutta, Nr. D 175, Nagri zone of the Bakrala Hills of Alipur

Dryopithecus giganteus n. sp. (Pilgrim 1915:27)
Dryopithecus giganteus Pilgrim (Gregory 1916:298)
Dryopithecus giganteus Pilgrim (Remane 1921:338)
?Dryopithecus giganteus Pilgrim (Remane 1922:165)
Dryopithecus giganteus Pilgrim (Gregory and Hellman 1926:74)
Dryopithecus giganteus Pilgrim (Colbert 1935:61)
Siyapithecus giganteus Pilgrim (Lewis 1937:145)

Dryopithecus giganteus Pilgrim (Weidenreich 1945:87)
Indopithecus giganteus Pilgrim (Koenigswald 1949:517; 1952:310)
Sivapithecus sp. (Hooijer 1951:93)

The right lower M_3 of Alipur was regarded by Remane (1922) as being closely allied to *Pongo* or as belonging to *Pongo* itself. Gregory (1916) wrote that *Dryopithecus giganteus* "appears to be rather closely allied to the ancestors of the chimpanzee." Lastly, Koenigswald (1949) expressed the interesting opinion that the M_3 dex. of Alipur and the P_3 of Haritalyangar do not show any special affinities to the recent Pongidae (*Indopithecus* n. gen.) but possibly to *Gigantopithecus* Koenigswald.

P_3 dex., Indian Museum, Calcutta, Nr. D 190, Nagri zone of the Siwaliks, Haritalyangar, Simla Hills

Sivapithecus indicus Pilgrim 1910 (Pilgrim 1915:45)
Sivapithecus indicus Pilgrim (Remane 1922:167)
Sivapithecus indicus Pilgrim (Gregory and Hellman 1926:21)
Sivapithecus himalayensis n. sp. (Pilgrim 1927:16)
Sivapithecus himalayensis Pilgrim (Colbert 1935:68)
Sivapithecus indicus Pilgrim (Lewis 1937:144)
Indopithecus giganteus (Pilgrim) (Koenigswald 1949:517)
Cf. *Pongo pygmaeus* (Hoppius) ssp. (Hooijer 1951:94)

In a more recent paper, Hooijer (1951) draws attention to the morphological specialization of the D 190 premolar at the Indian Museum, Calcutta, and considers the specimen to be closely allied to the *Pongo* line of pongid evolution. "Hence it is extremely improbable," he adds, "that this Mio-Pliocene tooth, which has the same size and structural character as the recent P_3 of the orang-utan, belongs to *Pongo pygmaeus*. The Haritalyangar premolar shows us only that, besides *Dryopithecus* and *Sivapithecus*, there was an ape in the Nagri formation of the Siwaliks which in its P_3 had already acquired the specialization typical to the orang-utan of today." The morphological correspondence is indeed striking, but we have to agree with Hooijer in not determining this isolated P_3 as *Pongo* s. str.

M^3 dex., Indian Museum, Calcutta, Nr. D 188, Chinji zone, Lower Siwaliks, Chinji

Palaeosimia rugosidens n. gen. (Pilgrim 1915:29)
Palaeosimia rugosidens Pilgrim (Gregory 1916:286)
Palaeosimia rugosidens Pilgrim (Remane 1921:338)
Pongidae gen. et sp. indet. (Remane 1922:163)
Palaeosimia rugosidens Pilgrim (Gregory and Hellman 1926:18)
Palaeosimia rugosidens Pilgrim (Colbert 1935:67)
Sivapithecus sivalensis (Lydekker) (Lewis 1937:143)
Palaeosimia rugosidens Pilgrim (Weidenreich 1945:89)
Palaeosimia rugosidens Pilgrim (Badoux 1959:118)

In describing this molar, Pilgrim (1915) had already observed that the tooth "distinctly foreshadows that of the orang, in its general pattern and in the characters of the enamel folds and wrinkles, the differences all being obviously primitive

characters" (Gregory 1916). This view has also been accepted by more recent authors, but the scanty material—only one tooth—hardly makes for absolute certainty. Summarizing, we may state that there is a distinct break in the fossil documentation of the earlier history of the genus *Pongo* (due to lack of fossil materials) within the lower middle Pleistocene (Lengchaishan, Djetis), and the connection of the genus *Pongo* with other known fossil genera still remains hypothetical, although *Palaeosimia* seems, according to the fossil material known today, to be the most likely ancestor of this line.

DISTRIBUTION OF PLEISTOCENE *Pongo* (FIG. 1)

The pleistocene distribution-area hitherto known from fossil records seems to be only a part of the area once inhabited by early *Pongo;* we may confidently infer that pleistocene *Pongo*-populations also were living in the more westerly parts of southern Asia (Burma, India), as is suggested by corresponding pleistocene faunal associations in both areas. The northernmost border (cf. southern China) of late pleistocene *Pongo* distribution on the continent, too, does not seem to correspond with the same border in middle and early middle pleistocene times. Lastly, the pleistocene distribution-area seems to be only a part of the suggested mio-pliocene area of early evolution of the *Pongo* line.

Discoveries in Hang-Hum Cave, Luc-Yen, Province of Yen-Bai during recent field research of the DR Viet Nam/DDR expedition have proved that the animal still lived in northern Viet Nam in post-pleistocene times.

TAXONOMY OF FOSSIL AND SUBFOSSIL *Pongo*-POPULATIONS

In 1948 Hooijer (1948:280) erected on the fossil *Pongo*-teeth of the Hoshantung Cave (China) a new subspecies *Pongo pygmaeus weidenreichi* (Holotype: right lower caninus, cf. Weidenreich 1937:figs. 61 and 258). The fossil horizon was suggested as corresponding to the lower or middle Pleistocene. The differences mentioned by Hooijer are very minute, and Badoux (1959:118) questioned this subspecies as "premature." Even if we should accept a subspecies of pleistocene age not yet clearly defined by morphological and metrical differences, it is hardly possible to accept a second (subfossil) subspecies, *Pongo pygmaeus palaeosumatrensis* Hooijer 1948, that also has inadequate characterization.

SUMMARY

Because of the lack of fossil documentation it is today impossible to draw the outlines of the pleistocene history of the great Pongidae of Africa: *Pan* and *Gorilla*. In southeastern Asia, however, pleistocene remains of *Pongo* are on record and a review of the pleistocene history of *Pongo* is possible. In early middle pleistocene times a distinct break in the fossil record of *Pongo* is stated, though a connection with *Palaeosimia* is possible but hypothetical.

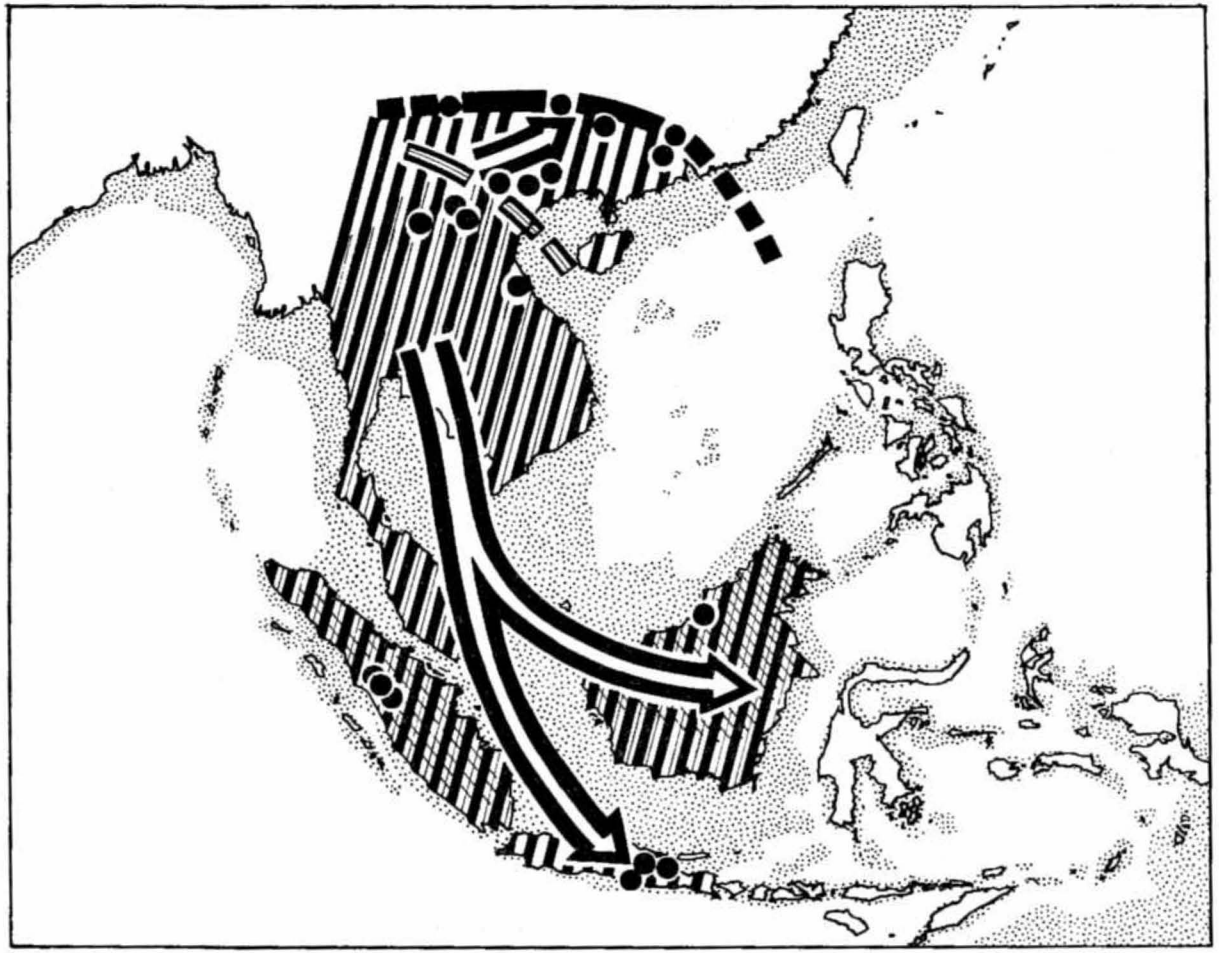

Fig. 1 Distribution of Pleistocene and Recent Orang-Utan.

Recent;

Subrecent (early post-Pleistocene);

Pleistocene;

northern border of Pleistocene distribution;

northern border of Subrecent (early post-Pleistocene) distribution;

fossil (or subfossil) locality;

direction of Pleistocene distribution.

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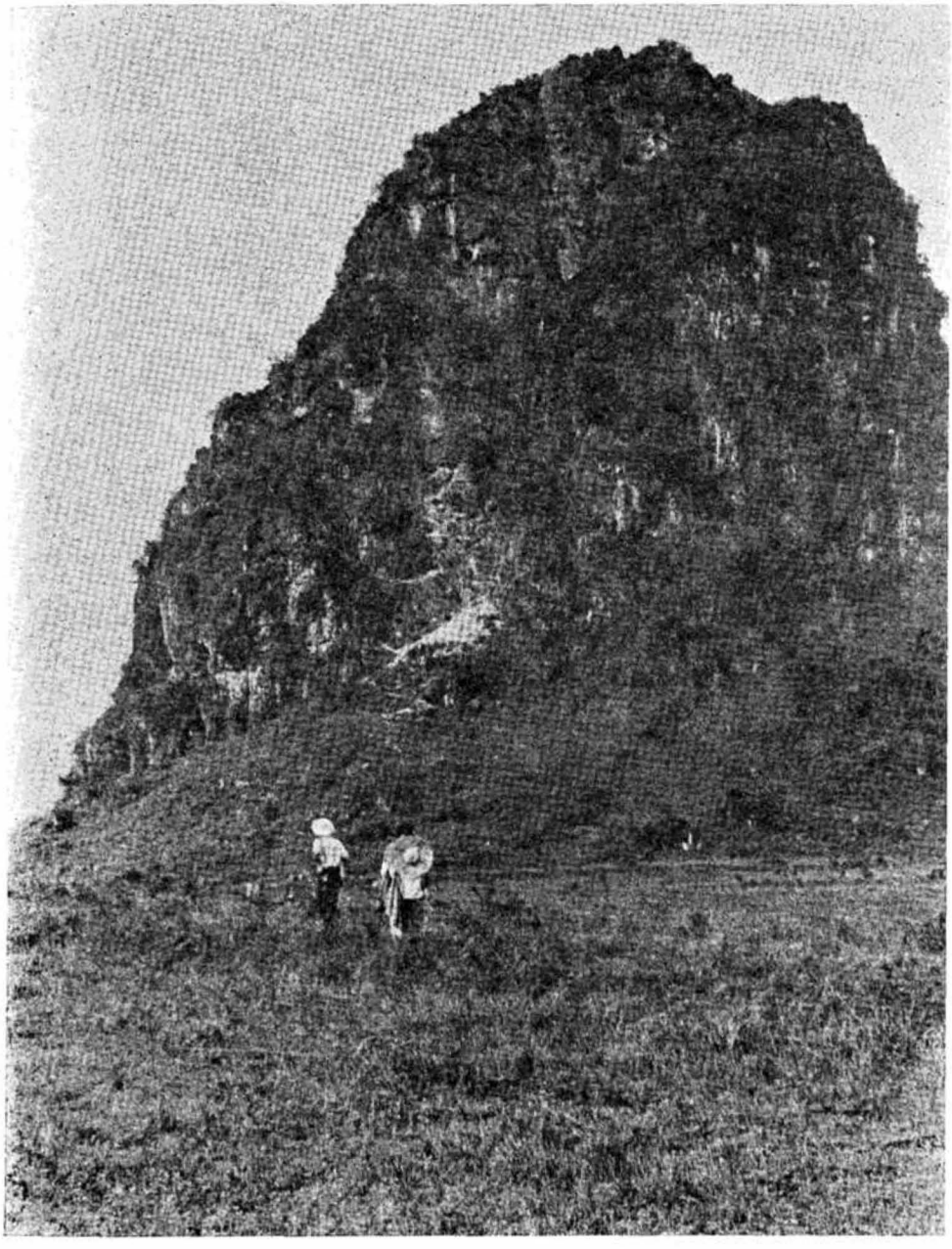

Plate I Lengchaishan, Kwangsi, China, type-locality of the *Pongo-Mastodon* associations, early-middle Pleistocene (photo: Kahlke).

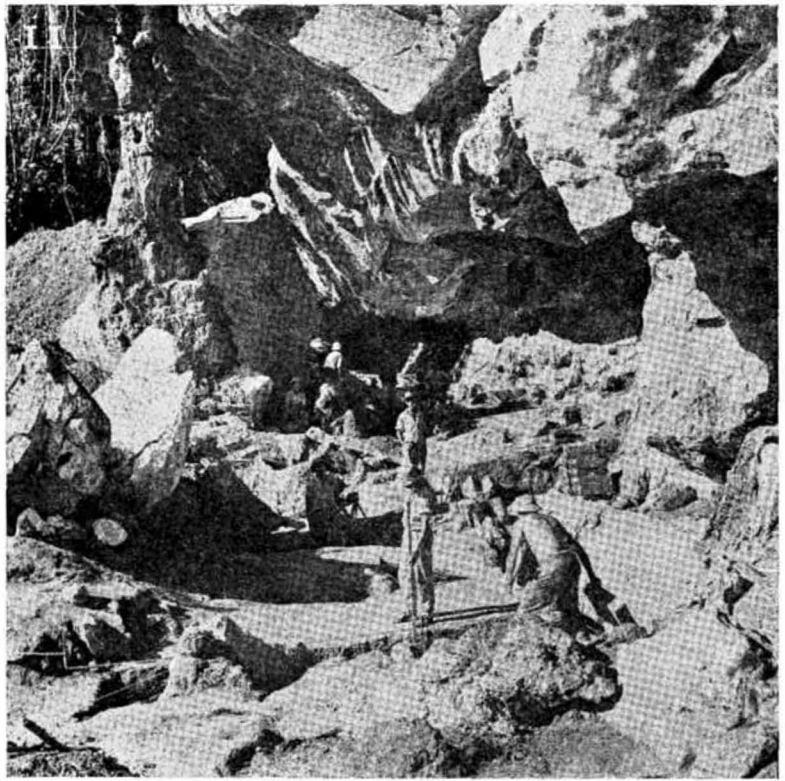

Plate II Hang-Hum Cave, DR Viet Nam, fossil locality of late-pleistocene and post-pleistocene *Pongo* (photo: Kahlke).

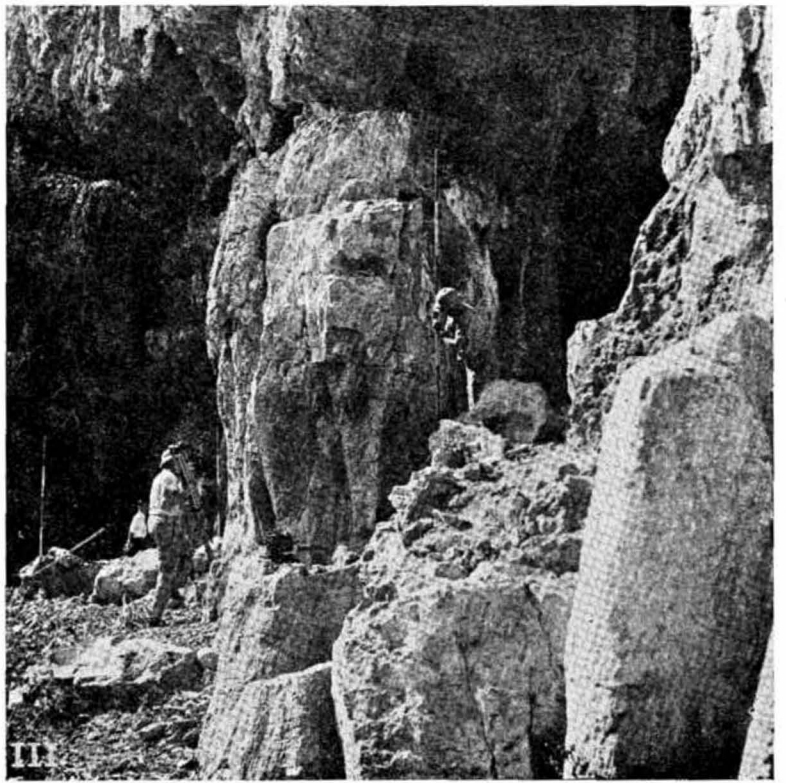

Plate III Tan-Van Cave, DR Viet Nam, fossil locality of an upper-middle pleistocene fauna with *Pongo* (photo: Kahlke).